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Research article

Island biogeography theory and the assembly patterns of native versus non-native forest insects

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Forest tree diversity helps shape the assembly of herbivorous insect communities in forests worldwide, and Island biogeography theory explains the role of tree range area as a driver of variation in native insect richness per tree species. However, it is unclear if these biogeographical principles apply to non-native insect herbivores. We created an extensive list of tree–insect associations for tree species native to Palearctic Europe bioregion, and investigated how both native and non-native insect herbivore species richness per tree may be influenced by various factors including the range area of the tree and the tree type (conifer or angiosperm). Models were further subsetted to compare drivers for the richness of different feeding guilds (folivores, sap feeders or wood borers) and host breadth (specialist or generalist). Tree range area had a positive effect on native, but not non-native, insect species richness per tree, while non-native richness was affected by host type and had a positive correlation with native herbivore richness on the same tree species. Host breadth grouping did not influence the difference in the effect of tree range on native versus non-native insect richness, but native folivores had a stronger relationship with range distribution area compared to the other groups. We conclude that the assembly of non-native herbivorous insect species on trees occurs through fundamentally different mechanisms than the co-evolutionary processes proposed by the framework of Island biogeography theory.

Keywords: community assembly, forest insects, herbivore, host breadth, host range area, Island biogeography theory, species richness

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Introduction

Much of the world's diversity can be explained by geographic barriers that have compartmentalized species assemblages such that faunal and floral species radiation has occurred in partial isolation across trophic levels (Thompson 2005). However, another factor driving diversity is the evolutionary specialization of insects on plants through reciprocal adaptations that has resulted in insect diversity tracking plant diversity (Gilbert and Raven 1973, Strong 1979, Dinnage et al. 2012, Forister et al. 2015). Hence, species diversity of insects feeding on an individual plant species is an emergent property of reciprocal adaptations.

Plant size is an important functional trait associated with insect richness, with large plants (i.e. trees) supporting a higher diversity of herbivorous insects than small ones (i.e. grasses) (Simberloff and Wilson 1969, Lawton 1983). In a landmark study, Southwood (1961) documented that the richness of insect species associated with British tree species was proportional to the land area occupied by that tree species. Similar species richness–area relationships have been documented for a variety of insect groups occurring on trees in various geographical regions (Opler 1974, Cornell and Washburn 1979). These relationships can be explained by the Island biogeography theory (MacArthur and Wilson 1967), with trees analogous to islands; the probability of any tree species being 'colonized' by an insect herbivore depends on the frequency of random encounters that increase the likelihood that the insect will adapt to the chemical and physical characteristics of a host species (Janzen 1968). The resulting positive relationship between tree range area and insect species richness is thus analogous to the species–area relationship, which is perhaps the most recognized biogeographical pattern in the world (Lomolino 2000).

Globalization has broken down barriers responsible for compartmentalizing the world's biota and species are increasingly introduced to communities with which they have had no prior evolutionary contact. Sometimes these novel species interactions result in explosive population growth in non-native species, which can be attributed to their lack of coevolution with other species in their new habitat (Facon et al. 2006). In the case of the relationship between trees and insect herbivores, such novel interactions can arise in three ways: by the invasion of non-native insects that feed on native trees, by the introduction of non-native trees that are fed upon by native insects, and by non-native insects feeding non-native trees. Though all types of novel associations can result in ecological disequilibrium in which insects cause severe impacts on host trees (Crous et al. 2017), here we limit our focus to the case of invasions of non-native tree-feeding insects. In such invasions, the lack of evolved bottom–up or top–down interactions can facilitate the formation of epidemic populations that cause regional host declines in the invaded range (Gandhi and Herms 2010, Brockerhoff and Liebhold 2017). Identifying the factors that make certain tree species more prone to herbivory by non-native insects is important for predicting the spatial distribution of non-native herbivores. In addition, understanding the potential species richness of non-native species on particular tree species could be part of biosecurity measures intended to protect native forests (Nahrung et al. 2023).

Here, we present an extensive database of insect–host associations for native tree species in Europe to compare the assembly of non-native and co-evolved native insects on trees. We focus on the role of host range area as a driver of herbivore species richness per tree species, and test whether this differs between native and non-native insects, feeding guilds, and host specialists and generalists. For example, it may be expected that guilds with higher dispersal abilities, and/or groups that utilize more host species, might exhibit a weaker species–area relationship because they are less constrained by the geographic distribution of a single host tree. If insect species richness per tree were, overall, strongly driven by host range area, it would be expected that the relationship would be observable for both native and non-native species richness. Specifically, we examine whether: 1) non-native herbivore communities on trees reflect the biogeographical assembly theory and resemble that of native species (i.e. higher species richness on trees with larger range areas); 2) the relationship between tree species range area and herbivore richness varies among insect guilds between native and non-native insects; and 3) the relationship between tree species range area and herbivore richness differs between host specialists and generalists between native and non-native insects.

Material and methods

Data collection

An extensive list of tree species (n = 77) native to Europe was compiled. The list originated from the European atlas of forest tree species (San-Miguel-Ayanz et al. 2016), but with non-native tree species removed, and all trees were classified as either a conifer or angiosperm. This list does not include all tree species native to Europe, but does include species with the largest range areas that are documented in national forest inventories. For each tree species, a list of insects known to utilize that species as a host was compiled using nine sources: Blackman and Eastop 1994, Smith and Roy 2008, Robinson et al. 2010, Pickering 2011, Kunca et al. 2013, Jendek and Poláková 2014, García Morales et al. 2016, EPPO 2021 and Liljeblad 2021. None of these sources provided a complete census of herbivore species associated with each tree species, but they provide collections of published records, covering multiple herbivore groups (e.g. 'HOSTS – a database of the world's Lepidopteran hostplants') and areas of Europe (e.g. 'The database of British insects and their foodplants'), and when combined resulted in one of the most extensive databases of herbivore associates of trees in Europe (Trombik et al. 2024). Each insect species was then researched to determine its higher level taxonomy (order

and family), feeding guild (gall maker, folivore, reproductive plant feeder, sap feeder or wood borer), and whether it was native to Europe or non-native based on the Fauna Europea database (De Jong et al. 2014) and the International non-native insect establishment database (Turner et al. 2021). To account for incomplete data that may be generated by poorly studied trees, trees with less than 12 total insect species associated with them (n = 9 trees) were removed from the dataset. Lastly, each insect species was categorized as either a specialist or generalist at the host genus level, where a specialist was defined as an insect species that feeds on trees within the same genus, while a generalist has hosts in multiple genera. This classification was a post hoc determination based on the host(s) each insect utilized in our compiled database.

Accuracy of the dataset was ensured through multiple steps that involved the removal of: 1) insect species not considered herbivores (e.g. detritivores and parasitoids); 2) duplicate tree–insect pairs due to spelling errors (e.g. *Alebra wahlbergi* versus *A. wahlbergii*) or different Latin cases (e.g. *Phyllonorycter cerasicolella* versus *P. cerasicolellus*); and 3) subspecies if the species was already listed for the tree species (e.g. *Automeris io* and *Automeris io* subsp. *io*). In addition, insect species synonyms were identified, and subsequently removed, using the GBIF backbone taxonomy with the 'rGBIF' R package (Chamberlain et al. 2017).

The range area of each host tree species was estimated based on digital chorological maps for the main European woody species (Caudullo et al. 2017), which define continuous areas of occupancy of the species range. The tree range area across the Europe was computed from the fused areas of both native ranges and synanthropic occurrences outside the native range provided in the database using ArcGIS pro (ESRI 2015). For Pan-palearctic tree species that occur across both Europe and Asia (e.g. *Juniperus communis*), only the range in the European region was considered. The boundary between Europe and Asia was delineated by the Aegean Sea, the Turkish Straits, the Black Sea, the Greater Caucasus, the northwestern portion of the Caspian Sea, and the Ural Mountains. Major islands, such as Great Britain, Ireland and Cyprus, were also included in the study.

Structural equation model

All statistical analyses were performed using R ver. 4.2.0 (www.r-project.org). We used a simple structural equation model (SEM) to answer the question of whether non-native species richness is related to host tree area range directly or through the richness of the native community associated with the host tree species ('piecewiseSEM' package; Lefcheck 2016). This allowed us to partial-out candidate relationships (Table 1) that included potentially correlated variables, and highlight both the direct and indirect drivers of insect species richness per tree species (Fan et al. 2016, Lefcheck 2016). An SEM was fitted that included counts of all native and non-native insect species, tree type and host range area. Because species richness was recorded as count data, candidate relationships were modeled as negative binomial generalized linear models within the SEM. Conservative p-values were used to calculate path significance and relationships that were found to be non-significant during the first round of SEM fitting were deemed to include unnecessary parameters and deleted to create a simpler and more parsimonious model.

Generalized linear mixed models

We used generalized linear mixed models (glmm) to determine whether the relationship between native or non-native insect species richness and host tree range area also varied by herbivore guild and/or diet breadth. A negative binomial distribution was selected for model fitting because the response variable (species richness per tree) was count data and suffered from overdispersion ('glmmTMB' package; Brooks et al 2017). The explanatory variables included in the model were host tree range area (continuous variable), nativeness (fixed factor, two levels; native and non-native), and diet breadth (fixed factor, two levels; generalist and specialist) or feeding guild (fixed factor, three levels; folivore, sap feeder and wood borer). The random effect variables included were the tree species and host type (conifer or angiosperm). We included all possible interaction terms in the model and used a type II ANOVA ('car' package; Fox and Weisberg 2011) to bring

Table 1. Relationships tested in structural equation model regarding factors that influence the species richness of native and non-native insects on European tree species (Fig. 2). Shaded variables (non-significant) were removed to create a more parsimonious model (Fisher's C = 5.187; p = 0.269 df = 4; χ^2 = 2.53, p = 0.282, df = 2).

Models	Predictor variable(s)	Estimate (SE)	p-value
1) Non-native richness ~ Tree type + host range area + Native richness			
	Tree type	–	0.006
	Type = conifer	1.52(0.15)	< 0.001
	Type = Angiosperm	2.01(0.08)	< 0.001
	Host range area	−0.96(0.8)	0.379
	Native richness	0.001(0.001)	0.11
2) Native richness ~ Tree type + host range area			
	Tree type	–	0.34
	Type = conifer	4.09(0.15)	< 0.001
	Type = Angiosperm	4.50(0.10)	< 0.001
	Host range area	0.50(0.1)	< 0.001
3) Non-native richness ~ ~ Native richness (correlation)		0.35	0.002

forward the model that only contains significant predictors (Crawley 2012) starting with the highest level (three-way) interaction. The 'ggeffects' package (Lüdecke 2018) was used to extract the model predictions for visualization (R package 'ggplot2', Wickham 2016).

Results

Descriptive statistics

A total of 68 tree species (49 angiosperms and 19 conifers) native to Europe were used in the analyses (Supporting information). These species were in 31 genera and 17 families. The conifer tree species with the smallest range area included in our study was Serbian spruce *Picea omorika*, which was only found across 489 km^2, whereas common juniper *Juniperus communis* covered 6 572 418 km^2 in Europe. Common aspen *Populus tremula* had the largest area for angiosperms (8 040 092 km^2), while horse chestnut *Aesculus hippocastanum* had the smallest range of the angiosperms included in our study (4929 km^2) (Supporting information).

Overall, 2848 herbivorous insect species were recorded in the database, with 100 of these being non-native to Europe (Supporting information), resulting in a final dataset of 7598 tree-insect pairs. Non-native species in Europe invaded from five different biogeographic realms that included all realms except Australasia and Antarctica. Slightly more than half were native to Palearctic Asia (51%) followed by the Nearctic (26%), Afrotropic (9%), Neotropic (8%) and Indomalaya (6%). The most commonly represented native insect families on European trees were Curculionidae (weevils, bark and ambrosia beetles; Order Coleoptera; n = 738 tree–insect pairs), Geometridae (geometer moths; Order Lepidoptera; n = 690 pairs), and Aphididae (aphids; Order Hemiptera; n = 661 pairs). For non-native insects, the most represented families were Curculionidae (n = 84 pairs), Cerambycidae (longhorn beetles; Order Coleoptera; n = 76 pairs) and Diaspididae (armored scale insects; Order Hemiptera; n = 60 pairs). On average, there were 105.06 (± 12.21 SE) native insect species per tree species recorded versus 6.68 (± 0.53) non-native species (Fig. 1a). Angiosperms had 57% more native insect species compared to conifer species ($\bar{x}$ = 116.86 ± 15.28 versus $\bar{x}$ = 74.63 ± 17.61) and the proportion was somewhat higher (64%) for non-native species on angiosperms compared to conifers ($\bar{x}$ = 7.49 ± 0.65 versus $\bar{x}$ = 4.58 ± 0.65). Pedunculate oak *Quercus robur* had the most recorded native species with 423, while Scots pine *Pinus sylvestris* had the most (n = 285) herbivore species amongst conifers (Supporting information). European trees with the fewest native insect species found in the resources used included narrow-leaved ash *Fraxinus angustifolia* (n = 8), and European nettle tree *Celtis australis* (n = 11) (Supporting information). The tree species with the highest number of non-native insect species was olive *Olea europaea*, which had 27 non-native species, whereas two tree species, cade juniper *Juniperus oxycedrus* and European hop-hornbeam *Ostrya carpinifolia*, had none (Supporting information).

The majority of native species on both conifers (59%) and angiosperms (64%) were classified as host genus-level specialists. Conversely, most non-native insects were classified as generalists (77% for conifers and 55% for angiosperms) (Fig. 1c,). The most polyphagous non-native species was the black stem borer *Xylosandrus germanus*, an ambrosia beetle that utilized 33 European tree species. Feeding guild compositions varied between native and non-native species, with the majority of native insect species (37% for conifers and 56% for angiosperms) being folivores, whereas most of the non-native species (45% for conifers and 72% for angiosperms) were sap feeders (Fig. 1d, 3a). In addition, the number of non-native wood borers in Europe exceeded the number of non-native folivores per tree for both conifers and angiosperms (Fig 1d). Given the minimal number of non-native gall makers and reproductive plant feeders in the database, these insects were not included in the analyses regarding feeding guild.

Species–area relationships

A cursory view of the relationship between insect species richness per tree and the tree host range area shows a different pattern between native and non-native species (Fig. 1b). This was supported by piecewise SEM, which indicated that the species richness of native insects is strongly affected by the range area of the host tree (Fig. 2). In contrast, there was no direct effect of host range area on non-native richness, but there was a positive correlation (r = 0.35) between native and non-native insect richness (Fig. 2). While tree type (conifer or angiosperm) has a significant direct effect on non-native insect richness (estimate = 1.52 ± 0.15 for conifers and 2.01 ± 0.08 for angiosperms, p = 0.006), no effect of tree type was found on native insect richness (Fig. 2).

Influence of insect feeding guild

The generalized linear mixed model had a significant three-way interaction, which indicates that there is a difference in how tree range area affects native versus non-native insect species richness, and this difference is affected by insect feeding guild (p = 0.008; Fig. 3b, Supporting information). All feeding guilds show positive relationships between both native and non-native richness and host range area. However, for both folivore and sap feeder species richness, the slope for native species richness and host range area is steeper (0.87 and 0.18) compared to non-native species richness (folivore: −0.04 and sap feeder: 0.09) and host range area. Wood borer species richness shows the opposite pattern, where the positive slope of the relationship with host range area is similar for non-native species richness (0.09) compared to native species richness (0.02) (Fig. 3b).

Influence of insect diet breath

Host breadth type did not affect the difference in how tree range area affects native versus non-native insect species richness (p = 0.52; Fig. 4b, Supporting information). There was a

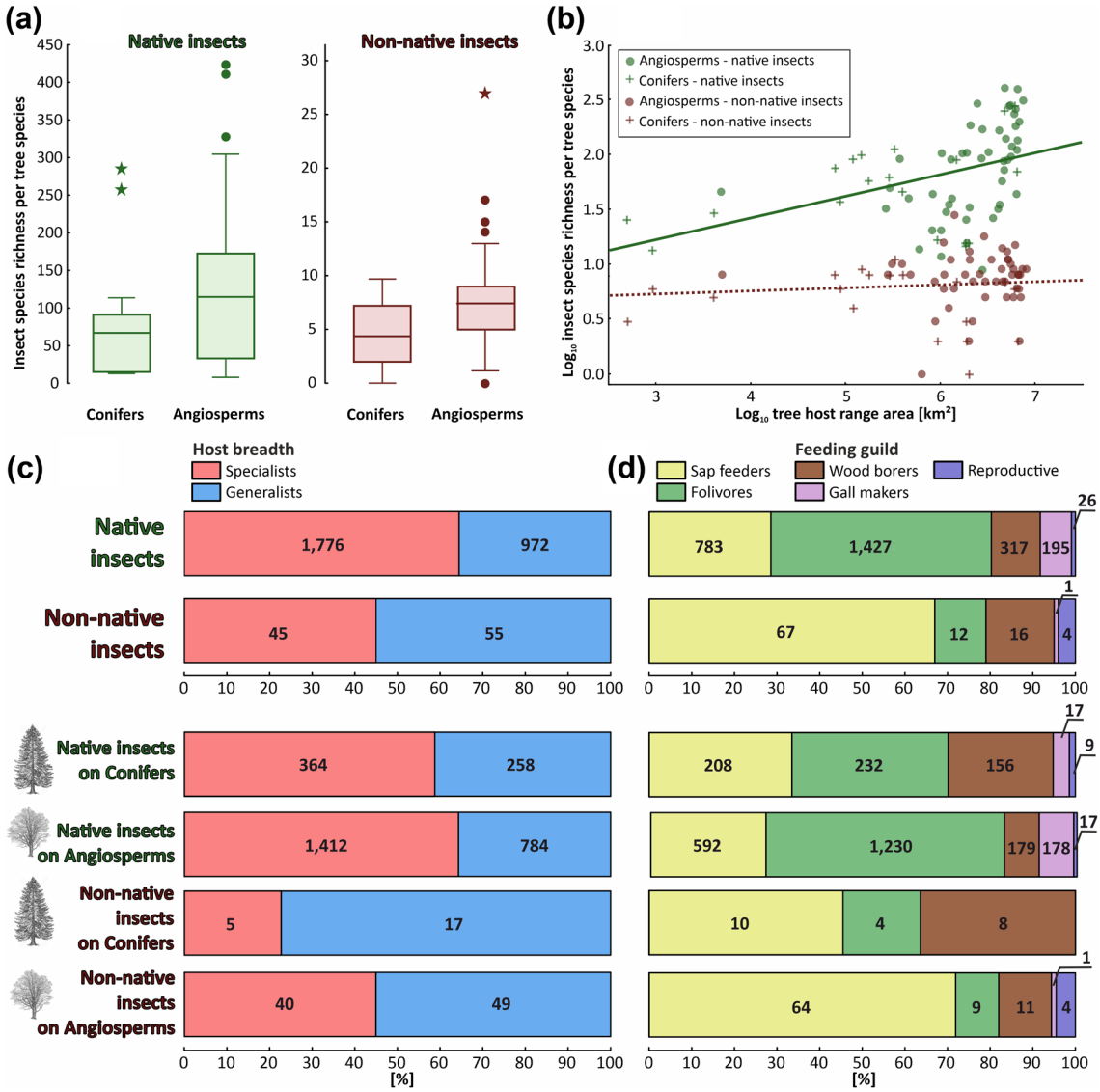

Figure 1. (a) Insect species richness per tree species for conifers and angiosperms, and native and non-native insects (horizontal line = mean; box = interquartile range; whiskers = non-outliers; circle = outliers; stars = extreme outlier trees). (b) Relationship between insect species richness per tree species and tree species range area (log-transformed). (c) Composition of insect species based on host breadth classes. (d) Composition of insect species based on feeding guilds. Numbers within bars represent the sample size of that group.

significant two-way interaction between nativeness and host breadth ($p < 0.001$), with more generalists present among non-native insects on trees compared to native insect species (Fig. 4a, Supporting information). In addition, native species richness showed a strong positive relationship (slope: 0.51) with the host range area regardless of whether they were generalists or specialists compared to non-native species diversity (slope: 0.12).

Discussion

Throughout the world, there is substantial variation in the numbers of insect species that use individual tree species as hosts. Understanding the factors that determine the species richness of herbivorous insects on different tree species is a question that has received considerable attention during the last 70 years. We provide clear evidence that native insect herbivore species richness on European trees is positively related to tree range area (Fig. 1, 3). Other studies have reported similar species area relationships for native insects and tree species in specific regions (Southwood 1961, Cornell and Washburn 1979, Brändle and Brandl 2001). However, this is the first report to do so at a continental/bioregion scale, as well as to examine this relationship with non-native insect herbivores.

With strong support for the island analogy, and increased probability of new plant–insect associations due to tree

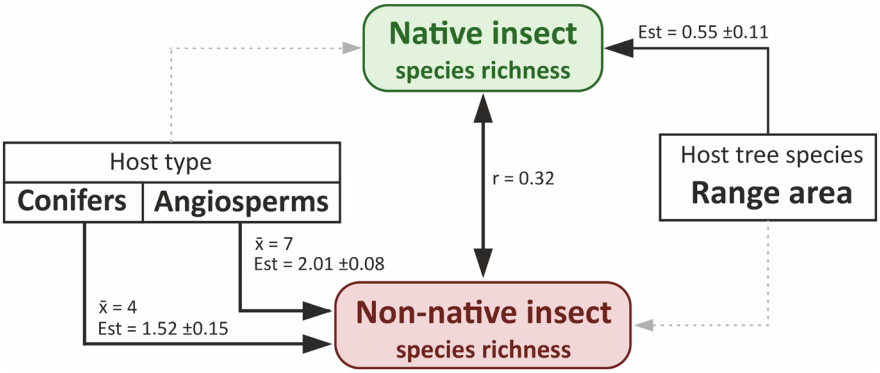

Figure 2. Structural equation model (SEM) of insect species richness. Significant pathways ($p < 0.05$) are represented by solid arrows; dashed arrows represent tested, but not significant pathways.

apparency, it would be expected that non-native insect herbivore richness would also be correlated to host range area. However, non-native herbivore species richness did not have the same relationship with tree range area as native richness on these same European trees (Fig. 2–4b). This suggests a fundamental difference between non-native and native insect community assembly mechanisms. Evidence indicates that most tree-feeding non-native insects first establish in urban or semi-urban areas (Branco et al. 2019, Ward et al. 2019), most likely due to the presence of ports of entry, and subsequently they spread to forested environments. Consequently, most first establishment events are unlikely in uninhabited forests. Non-native insects might therefore experience different selection pressures that could explain why host tree area has little or no effect on non-native insect herbivore richness. The only group of non-native insects for which richness had a steeper positive relationship with their tree host range area compared to the native insects in the same group were wood-boring insects (Fig. 3b). One possible explanation for this could be due to the widespread cross-country transportation of wood packaging material that could harbor cryptic and long-lived larval stages of wood-boring insects, increasing

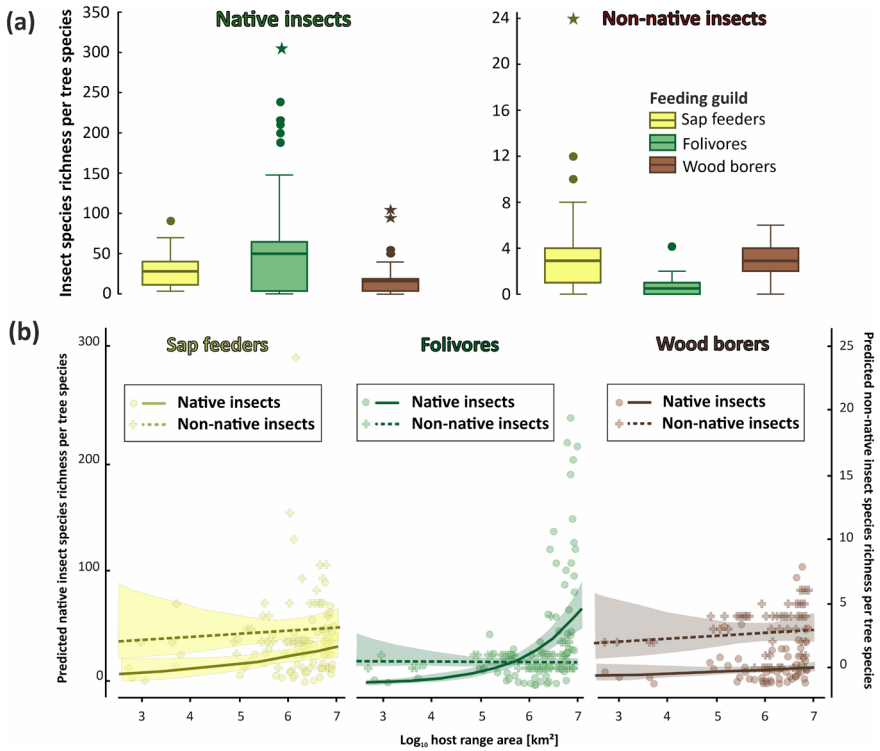

Figure 3. Results of generalized linear mixed model explaining the variability in herbivore species richness as a function of nativeness, feeding guild, and host range area. (a) Insect species richness per tree species for the three main feeding guilds, and native and non-native insects (horizontal line = mean; box = interquartile range; whiskers = non-outliers; circle = outliers; stars = extreme outlier trees). (b) Predicted herbivore species richness per feeding guild for native and non-native insect groups.

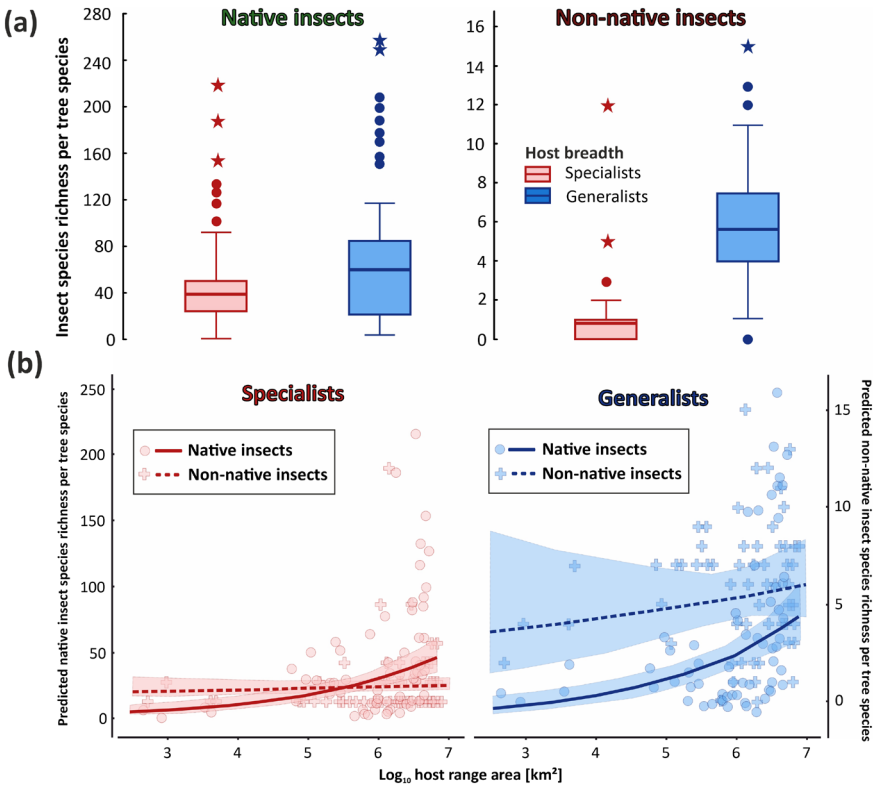

Figure 4. Results of generalized linear mixed model explaining the variability in herbivore species richness as a function of nativeness, host breadth (specialists or generalists), and host range area. (a) Insect species richness per tree species for host breadth categories, and native and non-native insects (horizontal line = mean; box = interquartile range; whiskers = non-outliers; circle = outliers; stars = extreme outlier trees). (b) Predicted herbivore species richness per host breadth category for native and non-native insect groups.

their likelihood of spread to more rural and forested areas, away from initial ports of entry.

The SEM indicated a weak positive correlation between overall native and non-native insect species richness (Fig. 2). The Biotic resistance hypothesis predicts that systems with high species diversity are more resistant to invasion because a higher number of potential niches are already filled (Elton 1958). This would indicate that within an ecosystem there should be a negative correlation between native and non-native species richness. However, studies testing this hypothesis have found conflicting results, with many, including this study, supporting the opposite relationship (Fridley et al. 2007, Peng et al. 2019). Most of these previous studies have focused on plant species richness and the few studies analyzing insect species have generally found a positive relationship between native and non-native species richness (Borges et al. 2006, Marini et al. 2011). In one exception, Liebhold et al. (2018) found no connection between native and non-native species richness among regions; however they found that both were strongly driven by plant richness. These studies have exclusively analyzed species richness of geographical areas (e.g. islands) so our analysis relating native to non-native species richness per host plant, rather than land area, is unprecedented.

We found that trees with the richest native insect herbivore assemblages appeared to be the most prone to invasion by non-native insects. The positive correlation between native and non-native herbivore species richness on individual European trees could be the result of variation among tree species in bottom–up mechanisms associated with tree defenses; trees attacked by a high number of herbivores may allocate more resources towards tolerance to herbivory rather than costly resistance traits needed to combat different feeding guilds, patterns, positions, etc. Previous studies have found that native insect species richness on trees can be explained by host traits other than their range area including tree size (Strong and Levin 1979, Brändle and Brandl 2001) and phylogenetic isolation (Kennedy and Southwood 1984, Grandez-Rios et al. 2015). It is likely that these traits have similar effects on the ability of both native and non-native insects to utilize individual tree species, resulting in the observed correlation in native and non-native insect species richness.

Overall, angiosperms supported more species of both native and non-native insect herbivores than did conifers (Fig. 1a). Conifers are an evolutionarily older plant group compared to angiosperms, and have evolved extensive chemical defenses that may repel more species of insects (Strong et al. 1984). The diversification of angiosperms around 225–240 Mya is believed to have been a major driver of adaptive radiation and diversification of insect herbivores on them (Wilson et al. 2013, Zeng et al. 2014). In particular,

beetles (Order Coleoptera) are the most diverse group of insects globally (17% of the herbivorous insect species in our database were in this group) and the diversification of angiosperms is believed to have been the driving force behind this diversity (Farrell 1998, Barraclough et al. 1998). The higher richness of both native and non-native insects on individual angiosperm species (Fig. 1a) suggests that angiosperms provide more ecological niches to be exploited compared to conifers. Brändle and Brandl (2006), who found that the communities of insects feeding on conifers in Europe was largely distinct from communities on angiosperms, also support this hypothesis.

Sap feeders comprised a much higher proportion of non-native (67%) than native species (29%) richness (Fig. 1d). The over-representation of this feeding guild amongst non-native species has also been observed in other global regions (Yamanaka et al. 2015, Liebhold et al. 2016, Mech et al. 2020a, b). This may be related to both their high incidence in invasion pathways (Smith et al. 2007, Liebhold et al. 2012) and high frequency of asexual reproduction, which gives them a higher probability of establishing following introduction (Liebhold and Tobin 2008). We also found that the relationship between herbivore richness and tree range area varied among feeding guilds (Fig. 3b), with folivores having the strongest relationship. Tree species with larger range areas had more species of folivores present compared to rarer trees. Folivores tend to be more mobile than other guilds, especially sap feeders, which could factor into this difference.

In a global study, Forister et al. (2015) found that most herbivorous insect species are specialists. Our data supported this pattern for native insects, but non-native insects in Europe had a relatively higher proportion of generalists (Fig. 1c, 4a). Previous studies (Gougherty and Davies 2022, Wang et al. 2022) have also identified higher host breadth among non-native species, which may be due to a greater likelihood that generalists will find a host and establish when they arrive in a novel region. However, the relationship between herbivore richness and tree range area was not affected by host breadth (Fig. 4).

While many of the patterns observed here appear robust, it is worth considering several caveats. First is that patterns relating host range area to herbivore richness may be affected by variation in the intensity with which insect communities are sampled and reported among tree species. The number of species recorded on a host can be a function of the scale of area sampled (Palmer and White 1994), the time span of sampling, as well as their interaction (Adler et al. 2005). We also may have missed herbivore species if they were not included in one of the nine sources used to build our dataset. To compensate, we excluded nine tree species with the fewest number of herbivores, but it is likely that sampling error still had a small effect on the observed relationships. Another issue is that our classification of herbivores being labeled as either host genus-level specialists or generalists is influenced by the fact that we only sampled woody trees, so insects that also feed on herbaceous or woody, non-tree plant genera may be incorrectly classified as specialists when in fact they are generalists. In addition, the definitions of specialists and generalists are often ambiguous – here we defined a specialist as those that utilize a single host genus, but others may consider a specialist to be a species that utilizes a single host family (Bernays and Graham 1988). Because of this, there may be slight differences in results based on changes to the definitions. Lastly, time since invasion (and publication date of sources) could influence the number of recorded hosts for non-native insect species – recently introduced insect species may not have been exposed to all potential hosts yet.

Overall, our dataset of tree–insect pairs of Europe is a valuable compilation that can be used to answer other fundamental questions regarding the interactions of insect herbivores and their host trees. Future research could examine relationships for other continents, herbivore assemblages on non-native tree species, and host traits that could be influencing species richness.

Conclusions

Our results indicate that non-native insect herbivore richness per tree is not directly explained by the range area of host tree species, but there was a positive correlation to native herbivore richness on the same tree species, which does have a significant relationship with host area. Feeding guild was found to affect this difference, but host breadth was not important. We conclude that the community assembly of non-native herbivorous insect species on trees occurs through fundamentally different mechanisms than the co-evolutionary processes, such as those proposed by the theoretical framework of the Island biogeography theory, that drive native insect richness.

Speculations

Our observed correlation between the numbers of native and non-native insect species associated with each tree species merits further investigation. As described above, this correlation may arise from chemical and physical host traits that make certain trees better hosts and create more ecological niches to be exploited by either native or non-native herbivores. However, this correlation may also result from some aspect of the global biogeography of trees and herbivorous insects. Native tree species that are phylogenetically similar to trees in global regions that are well connected via invasion pathways, such as those between Palearctic Europe and Palearctic Asia where the majority of these non-natives were from, might be more susceptible to hosting insect species arriving from those regions. Phylogenetic similarity with co-evolved hosts is a well-known determinant of the utilization of novel hosts by insect herbivores. Consequently, when an invading insect encounters a novel tree species that is phylogenetically similar to its native host, that novel tree is more likely to be utilized as a host. As a result, certain tree species that are common in both source and invaded regions are

likely to support more species rich assemblages of both native and non-native insects.

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Data availability statement

Data were derived from public domain resources, and are available in article Supporting information or through the Dryad Digital Repository: https://doi.org/10.5061/dryad.3n5tb2rrx (Trombik et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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